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Comparing environmental influences on coral bleaching across and within species using clustered binomial regression

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ABSTRACT

Differential susceptibility among reef-building coral species can lead to community shifts and loss of diversity as a result of temperature-induced mass bleaching events. We evaluate environmental influences on coral colony bleaching over an 8-year period in the Florida Keys, USA. Clustered binomial regression is used to develop models incorporating taxon-specific responses to the environment in order to identify conditions and species for which bleaching is likely to be severe. By building three separate models incorporating environment, community composition, and taxon-specific responses to environment, we show observed prevalence of bleaching reflects an interaction between community composition and local environmental conditions. Environmental variables, including elevated sea temperature, solar radiation, and reef depth, explained 90% and 78% of variability in colony bleaching across space and time, respectively. The effects of environmental variables were only partially explained (33% of variability) by corresponding differences in community composition. Taxon-specific models indicated individual coral species responded differently to local environmental conditions and had different sensitivities to temperature-induced bleaching. For many coral species, but not all, bleaching was exacerbated by high solar radiation. A 25% reduction in the probability of bleaching in shallow locations for one species may reflect an ability to acclimatize to local conditions. Overall, model results indicate predictions of coral bleaching require knowledge of not just the environmental conditions or community composition, but the responses of individual species to the environment. Model development provides a useful tool for coral reef management by quantifying the influence of the local environment on individual species bleaching sensitivities, identifying susceptible species, and predicting the likelihood of mass bleaching events with changing environmental conditions.

1. Introduction

Differences in sensitivity of species to disturbance is known to be a major factor influencing abundance and diversity of ecological communities (Connell, 1978; Huston, 1994). Coral reefs have experienced extensive mortality over the past several decades as a result of temperature-induced mass bleaching events (Hoegh-Guldberg, 1999; Hughes et al., 2003; Obura, 2005). Coral bleaching results from the loss of symbiotic dinoflagellate algae (zooxanthellae, *Symbiodinium* spp.) or

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their pigments, and can lead to reductions in colony growth, disease resistance, and survival (Douglas, 2003). Recently it has been documented that corals differ in their susceptibility to bleaching (McField, 1999; Marshall and Baird, 2000; Obura, 2001; Baird and Marshall, 2002; Floros et al., 2004; McClanahan et al., 2004,2007a), and loss of coral cover in susceptible corals can lead to community shifts and loss of coral reef diversity (Loya et al., 2001). An important tool for coral reef management is the development of predictive models to aid in the identification of susceptible and tolerant coral communities and reef areas (Maina et al., 2008).

Sustained elevated sea temperatures during the warmest months of the year are a primary cause of mass bleaching, and increasing prevalence of coral bleaching has been attributed to rising ocean temperatures (Hoegh-Guldberg, 1999; Wilkinson, 2002; Sheppard, 2003). Historically, elevated sea-temperatures have been used almost exclusively to predict prevalences of mass coral bleaching (Goreau and Hayes, 1994; Goreau et al., 2000; Liu et al., 2005), but there is considerable variation in the degree of bleaching across spatial and temporal scales (West and Salm, 2003; Berkelmans et al., 2004; Obura, 2005). Two major factors that are known to affect bleaching intensity and should be incorporated to improve accuracy of predictive models are (1) interspecies variability in bleaching susceptibility and (2) local environmental conditions.

Incorporating information on coral community type (Wooldridge and Done, 2004) or relative densities (McClanahan et al., 2007b) into predictive models can improve the accuracy of bleaching predictions. However, the effect of temperature on the bleaching responses of individual species can vary over time (McClanahan et al., 2007a) and space (McClanahan et al., 2004). Local environmental factors interact with temperature in ways that either exacerbate bleaching or enhance coral resistance to bleaching. In particular, doldrum events and elevated solar radiation are sometimes associated with mass bleaching events (McField, 1999). Strong ocean currents mix warm surface water with cool deeper water and can lessen bleaching (Riegl and Piller, 2003; West and Salm, 2003; Wooldridge and Done, 2004; Manzello et al., 2007). Solar radiation, in the form of photosynthetically active radiation (PAR) or ultraviolet radiation (UVR), can exacerbate bleaching (Gleason and Wellington, 1993; Lesser and Lewis, 1996; Hoegh-Guldberg, 1999), but the amount of solar radiation to which coral are exposed may be reduced in deep (Riegl and Piller, 2003) or turbid (Goreau et al., 2000; Otis et al., 2004) waters. Coral exposed to high solar radiation, such as those in shallow water, may be more resistant to bleaching (Rowan et al., 1997; Spencer et al., 2000; Dunne and Brown, 2001; Brown et al., 2002). However, studies examining the effects of these environmental factors on coral bleaching are typically confined to a few species over a short period of time. To our knowledge, the relative contributions of local environmental variables to taxon-specific bleaching susceptibilities have not been adequately quantified.

Disentangling the effects of community composition and environmental variation is challenging because the local environment often defines the local community composition, yet individuals also may respond dynamically to changes in their local environment. We present a hierarchical suite of models, starting with a generic environmental model for all taxa and evaluating the improvement in bleaching predictions when community composition and taxon-specific effects are incorporated. First, model selection is used to develop a generic model of all coral taxa, beginning with a temperature-only model and incorporating water motion and solar radiation at the coral surface. We assess the ability of this environmental model to explain spatial and temporal variability in coral bleaching in the Florida Keys between 1998 and 2005. Next, we develop a hybrid model in which the magnitude of bleaching also depends on the relative abundances of coral species at a location. Finally, we develop taxon-specific models in which the effects of the environment are allowed to differ among species. Taxon-specific models are assessed as to whether they improve overall predictions of bleaching, and also allow us to interpret the differential effects of the local environment on each coral species.

2. Methods

2.1. *Study sites*

Survey locations were permanent sampling stations along the Florida Keys and Dry Tortugas coral reef tract, from 25°22′13″N, 80°8′23″W to 24°40′45″N, 83°2′13″W. Site locations, characteristics, and survey methods are detailed elsewhere (Santavy et al., 2001,2005). Briefly, survey locations were randomly selected from within five sectors of the South Florida Reef Tract in the Eastern and Western Keys known to contain hard coral bottom, approximately 5–10 km offshore. Locations contained at least 5% live coral cover, and ranged in depth from 1 m to 23 m. Coral colonies were counted within the 2-m circular band located 8–10 m from the center of each station, with a total survey area per station of 113 m^2. Between 24 and 48 stations were surveyed once annually from 1998 to 2005, excluding 2003, for a total of 287 surveys. Further details on coral community abundances measured at each station over time are presented in Santavy et al. (2006).

For each survey, coral colonies greater than 10 cm in diameter were identified to species and counted (Santavy et al., 2006). A core group of 16 coral species were consistently found in surveys (Table 1). *Montastraea annularis*, *M. faveolata*, and *M. franksii* were combined to form the *M. annularis* complex (Weil and Knowlton, 1994). *Mycetophyllia ferox*, *M. lamarkiana*, and *M. danaae* were infrequently observed and combined to *Mycetophyllia* spp. to increase the number of observations in taxon-specific models. Each colony was categorized as bleached if greater than 10% of the surface area was bleached. After August 1998, colonies were also categorized as severely bleached if greater than 50% of surface area bleached. Surveys were usually conducted from August to September, the time of year that ocean temperatures are warmest and mass bleaching events typically occur. We also include June 1999 surveys in analyses because our underlying hypothesis is that bleaching is temperature induced, therefore we include surveys conducted over a range of temperatures. We conducted separate analyses for bleaching (>10%; 287 surveys) or severe bleaching (>50%; 269 surveys) and obtained the same set of environmental variables in winning models for almost all cases, therefore we present results for the full data set.